THE REACTIONS OF AN ORB-WEAVING SPIDER, EPEIRA SCLOPETARIA CLERCK, TO RHYTHMIC VIBRATIONS OF ITS WEB.[1]

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WITH THREE PLATES.

I. INTRODUCTION.

The work reported in this paper was suggested by a chance observation[2] made in the summer of 1911. A fly was held close to one of the spiders without eliciting any response; when the fly's vibrating wing was allowed to touch a strand of the web, however, the response was instantaneous and positive. The spider ran to the fly and seized it. A vibrating rubber band held against a strand of the web caused a very similar response. During the summer of 1913 these spiders were studied more carefully in an attempt to determine: first whether the stimulus was vibratory in nature or must be considered to be due to some other force and second whether the response could be identified as a "tropism" or taxis.

II. MATERIALS AND METHODS.

At the Lake Laboratory maintained by the Ohio State University at Cedar Point, Ohio, the large orb weaving spider, *Epeira sclopetaria*, is very abundant, building its webs on the front porch and in the angles of the building and roof. The habit

[1] Contribution No. 42 from the Department of Zoology and Entomology, Ohio State University.

[2] The note of Boys (80) was not known to the writer until the larger part of these experiments had been carried out.

of the female of this species of remaining at the center of her web for long periods of time makes it a very convenient form to study in its normal surroundings.

This species builds its web in dead branches or in the angles of buildings where there is an abundance of small or medium sized insects. The web usually consists of 17, 18 or 19 relatively inelastic strands which radiate from a center like the spokes of a wheel. These radiating strands are attached at their outer ends to twigs or boards or to guys or stays which anchor several radii to the support. Surrounding the center of the web is an irregular network known as the hub and notched zone which serves as a resting place for the inhabitant of the web. For a short space outside the hub the radii are bare (the free zone) but beyond this is found the viscid spiral consisting of finer strands which are extremely elastic and are beaded with microscopic sticky drops which serve to hold and entangle the insect prey. It is probably the extreme elasticity of these spiral strands which allows them to detain a strong insect without being snapped, thus giving the spider time to reach the detained insect and complete its ensnarement by the addition of fresh silk from the spinneretts. The normal resting position of the female spider is with the head directed downward and the legs spread outward on the notched zone as is shown in Fig. 1. The method used to obtain this photograph and the others following is that used by Comstock ('12, p. 181). A female spider was placed on a dead branch held in the neck of a bottle which was set in a tray of water. During the first or second night the spider usually built a perfect web. The branch was then moved to the photographing table with as little disturbance as possible and placed in front of a soap box painted a dull black on the inside. Arranged in this way before the camera it was possible to take pictures showing the spider, web, and vibrator straw, and the various positions taken by the spider in the act of responding to the vibrator.

The size of the web varies from two inches in diameter, or even smaller when built by very young spiders, to eighteen inches or more when built by mature females. The male builds a web very much like that made by the female but as he has a roving disposition one is never sure that the same individual can be

located twenty-four hours later while the females often live for weeks in the same place, repairing the web every evening but not altering it materially.

In crawling across the web the spider always follows a radiating strand or at the edge of the web, one of the guy strands, and places its feet on the radii or on the junctions of the radii and spiral threads where the latter hold no sticky materials. The front feet are usually placed on the same radiating strand but the second and third pairs may be spread out on the two adjoining strands. It is possible for the spider to crawl rather swiftly along a single strand for a considerable distance, all eight feet using the same thread. In crossing the web the spider usually leaves behind a dragline which may remain across the web, adhering to it after the spider has returned to the center Some individuals on the other hand when they reach the edge of the web swing free, held only by the drag line up which they climb in returning to the center. Occasionally one finds both methods employed by the same individual. Most spiders are not skilful enough to cross the web several times without tearing out or snagging several of the segments of the spiral thread. When the web is violently disturbed the spider usually retreats to a niche or corner (the retreat) and remains there motionless unless again disturbed. Some individuals remain in the retreat instead of at the center of the web. When this is done one forefoot is placed on the trapeline leading to the hub and any activity of the web such as that produced by an entangled insect sends the spider like a flash down to the web. In this connection another fact may be noted; a spider outside the center of the orb always returns to the center, takes the normal position and then orients before it finds an entangled insect. This might be explained as due to the difficulty of crossing the web by any other path than by the radii. However, the inability to orient accurately in any other position than the center gives a clue to a more probable explanation. Individuals of the species *Epiera sclopetaria* will eat nearly any insects which happen to become entangled in the web. The food of those studied inside the screened porch consisted almost entirely of rather large flies of the genera *Musca*, *Sarcophaga*, and *Lucilia*. It is in the snaring of these flies that

this *Epeira* seems to be especially expert. When a fly strikes a web it often goes through, breaking out one or two spiral segments. If, however, it does not break through it hangs for a second, buzzing, then breaks one or two of the sticky strands and flies away. A fly seldom entangles itself to such an extent that it cannot get free inside of five seconds. A successful spider then must reach the fly in less than two or three seconds after it strikes the web. The actual capture of the fly is accomplished usually either by biting the fly and stunning it or by winding it with web. The entangled fly may be left where it struck or may be torn from the web, and carried attached to one of the spider's hind feet to the center of the web where it is thoroughly chewed and its liquid parts swallowed.

The apparatus used to produce rhythmic vibrations consisted of three tuning forks and an electric vibrator. One fork had a vibration rate of 100 double vibrations per second, another a rate of about 487 and the third was an adjustable fork with a large range of vibration rates but with very limited amplitude. The electric vibrator was a modified electric door bell in which the clapper was replaced by a long grass straw. The number of vibrations produced by this instrument could be varied to some extent by changing the tension of a spring and a regulator screw, while the amplitude of the vibration varied with the length of straw used. The vibration rate of the vibrator was obtained by comparing a tracing made by it on a sheet of blackened paper on a revolving drum with a simultaneous record made by the tuning fork giving 100 double vibrations per second. The electric vibrator was found to be more effective than a fork because it gave vibrations of equal intensity, *i. e.*, it did not run down. It had also another advantage in that it could be controlled by a switch held in the hand and could be operated at a distance from the operator. A stop watch was used to measure the time elapsing between the beginning of the stimulus and the arrival of the spider at the place where the straw touched the web.

III. Experiments.

1. *Experiments Using Rhythmic Vibrations.*

When the vibrator straw is placed against one of the spiral strands or against one of the radii and caused to vibrate the spider

orients instantly and advances along the nearest radius to the straw, seizes the straw with its mandibles and may spread web on the straw with the hind pair of feet (Fig. 3). This reaction is carried out in essentially this manner no matter where the straw may strike the web.

The orientation is so rapidly executed and is followed so closely by the forward locomotion that it is difficult to separate the two parts of the response. If, however, the vibrator is set in motion for a fraction of a second only the orienting is accomplished but the forward locomotion toward the vibrator does not follow. A second vibration while the spider is oriented calls forth the forward response and an attack on the vibrator (Fig. 3). The photograph reproduced in Fig. 2 shows such an orientation. If the first vibratory stimulus is not too long or is not followed by a second stimulus the spider usually returns to the resting position at the end of a few seconds. Some individuals, however, follow the orienting response by an interesting series of activities. The fore feet are placed on neighboring radii, drawn toward the animal's body and released suddenly. This release sets the web vibrating parallel to the spider's longitudinal axis. The spider then turns one space to the right or left and repeats the process until she has oriented through a complete circle and set every pair of radii in motion. The use of this activity is seen if there happens to be a captured fly or a piece of dirt in the web. When the two radii which pass on either side of the object are set vibrating the object is also set in motion but its motion is not of the same rate as that of the rest of the web and it sets up an echo or return vibration. To this the spider responds. A dead fly may be rediscovered in this way or a piece of dirt may be located and removed.

Responses to different frequencies show considerable variations and it is not possible to predict that a certain individual will respond in a definite way to a given stimulus. This variation in response ranges from instantaneous orientation and forward locomotion to a slow orientation and slow approach toward the vibrating point or it may happen that no sign will be given that the stimulus has been perceived. Roughly speaking a large spider responds most quickly to a vibration of considerable am-

plitude with a vibration rate of 24 to 300 per second. It was impossible with the materials at hand to construct a vibrator giving a high rate and having also a considerable amplitude, so recourse to steel wires and small forks was necessary. The large spiders did not respond well to wires and forks with high vibration rate and small amplitude but they did respond instantly to the vibrating wings of *Chrysops* (127 per sec.), *Microbembex* (208 per sec.), *Musca* (284 per sec.), where the amplitude ranged from 4 mm. to 10 mm. Small spiders responded quickly to vibrations ranging from 100 per sec. to 487 per sec. and even higher although the amplitude was very small. This difference in responsiveness between the young and old spiders is probably correlated with differences in size and rate of wing vibration of the insects which are ensnared and used as food by young and old. In general small insects have high wing vibration rates while the larger insects have lower rates of wing vibration (Packard, '03, p. 150). The smaller spiders eat small insects and the large spiders eat larger insects. The following species of insects were caught and eaten by *E. sclopetaria: Chrysops vitatus* (127 vibr. per sec.); *Calliphora vomitaria* (130 vibr. per sec.); *Microbembex monodonta* (208 vibr. per sec.); *Musca domestica* (284 vibr. per sec.). Many small midges (*Chironomus* and others) were eaten by the young spiders and occasionally by the adults. The vibration rate of these small midges is probably very high, judged by the high pitched note which they give out, but it was impossible at the time to determine its rate.

2. *Experiments Using a Y-shaped Vibrator.*

In order to determine whether the spider reacted to a single vibrating strand or to the center of a vibrating area of the web, a Y-shaped vibrator made up of insulated magnet wire was adjusted to the vibrator and arranged in such a manner that its ends touched the web at two places, 2 or 3 cm. apart. When the vibrator so adjusted was operated the spider responded readily, going to a point on the edge of the web midway between the two vibrating points and then after some slight hesitation going toward one or the other of the vibrator wires (see Fig. 4). If, however, these points of wire were more than 3 cm. apart the spider at the

center of the web usually hesitated, turning first toward one, then toward the other, finally orienting to one and attacking this by itself.

3. *Response in the Dark.*

In order to test the ability to respond in the dark the vibrator was set up late in the afternoon, the straw touching one of the radial strands of a web which was built in the frame of a window. The window was shaded on the outside by a heavy thicket. At 9:30 P.M. the room was so dark that a person standing inside could discern the outline of the window with the utmost difficulty. A flash of light from a pocket electric lamp showed that the female occupying the web was at the center of her web. The vibrator switch was closed and at the end of about four seconds the electric flash light showed the spider biting the vibrator straw in the same manner as that shown in Fig. 3. This experiment indicates that unless these spiders use rays of light which our eyes do not perceive, sight plays no essential part in the orientation to and the ensnaring of the prey.

4. *The Distribution of Vibrations through the Web.*

The distribution of vibrations as they travel across the web is of some theoretical interest. The following method for recording these vibrations was used with considerable success. A spider in its web was placed before the camera and made to respond to the vibrator repeatedly until it would respond no more. A photograph (Fig. 5) of 15 seconds' exposure was then made while the vibrator was in motion. The web was somewhat torn by the spider before it ceased to respond, but the photograph reveals by the thickening of the lines the distribution and amplitude of the vibrations in all parts of the web. The amplitude of the vibrations decreases rapidly from the periphery toward the center. The radial strand connected with the vibrator shows the greatest lateral displacement while the strands on either side of this show less and less disturbance as the distance away from the vibrator increases. A slight thickening of the spiral strands in a direction at right angles to the direction of the primary vibration can be noted on the segments directly across the center from the vibrator. The center of the web seems to be the part

least affected. If there is any motion here it is probably at right angles to the original vibration, that is, it is probably parallel to the spiders' long axis after orientation.

5. *Mutilation Experiments.*

The foregoing experiments coupled with careful observations on the spinning behavior of the orb-weaver lead to the conviction that the organs used in detecting the movements of the web are proably tactile, at least there are no other organs described which would seem to serve the purpose as well. There can be little doubt that sense hairs are very abundant on the legs, particularly on the tarsi of these spiders. These hairs have been described by Dahl (83), Wagner (88), McCook (90), and recently by McIndoo (11). The functions of these hairs have been interpreted in various ways, but little or no experimental work has been accomplished other than attempts to show that some spiders hear. Responses to sounds seem to have been observed only in those forms which build webs. It seems likely that responses in the web building forms are due to the vibrations of the air being picked up by the strands of the web (McIndoo, '11, p. 412). It was thought desirable to determine if possible the location of the sense-organs used in detecting vibrations. By careful manipulation with a pair of fine dissecting scissors it was possible to snip off one or more of a spider's legs without causing the spider to leave the web. It is necessary to use great care not to shake the web because an irregular shaking gives rise to the negative response, the spider running away to the retreat. The contrast between this insensibility to the amputation of legs and extreme sensitiveness to irregular vibrations of the web emphasizes the fact that these spiders receive most if not all of their mechanical stimuli through the web. These operations caused the spider to lose considerable blood but two or three hours usually sufficed to heal the wound. The stumps of the legs were always held up so that they did not touch the web.

Experiment 1.—After testing a spider to be assured that its responses were normal the two forelegs were cut off as near the middle of the metatarsus as possible. This spider immediately put the stumps of the forelegs into its mouth. The next morning

this spider was in its web. During the night the web had been repaired and a new spiral thread put on.

In recording the test made on this spider and those following, IX o'clock, XII o'clock, etc., refers to the position at the edge of the web which corresponds to the same hour on the clock face. Thus VI o'clock is used to designate the edge of the web which the spider normally faces when at rest, *i. e.*, directly downward.

Experiment 1.—Spider with both forefeet cut off. Fork giving 100 vibrations per second touching web in

III o'clock position spider reached fork 8 inches from center in 3 seconds.

IX o'clock position reached fork (8 in.) in 2½ sec.

VII o'clock position reached fork (8 in.) in 2½ sec.

Experiment 2.—Spider with third legs cut beween femur and patella.

IX o'clock position reacted 8 in. in 2¼ sec.

III o'clock position reacted 8 in. in 2¼ sec.

XII o'clock position reacted 8 in. in 7¼ sec.

This individual showed some difficulty in climbing, but oriented accurately.

Experiment 3.—Spider with second legs cut off at patella.

III o'clock position reacted 7 in. in 1½ sec.

XII o'clock position reacted 7 in. in 1½ sec.

X o'clock position reacted 7 in. in 1½ sec.

Experiment 4.—Spider with fourth legs cut off at patella. Reactions entirely normal as given above.

Another set of experiments which need not be detailed were carried out. In these the right first leg and left fourth leg were cut off and other similar combinations were made. In all cases orientations and the locomotion following were entirely normal except for the slight difficulties in locomotion which might be expected. These experiments indicate that the sense organs used in reacting to the vibratory stimuli are not restricted to any one pair of legs below the metatarsus. There are two possible distributions of sense hairs which would seem to make possible the reactions detailed above; the sense organs may be confined to the feet, where they come in contact with the web or they may be located on the legs or body in such a manner that they pick up

the vibration of the whole leg or whole body. Hinged sensitive hairs uniformly scattered over the body might answer this purpose. It seems most likely, everything considered, that the particular sense organs used are on the tarsi of each leg and come in contact with the web. It is difficult to conceive that an animal whose feet are not extremely sensitive could travel on or manipulate the delicate strands of these orb-webs.

IV. Discussion and Summary.

It is maintained in this paper as in a previous one (Barrows, '07) that an animal exhibits a "tropism" or better a taxis, "when under the influence of [chemical] stimuli acting unilaterally they move toward or away from the source of the stimulus" (Verworn, '99, p. 249). It has been shown above that *Epeira sclopetaria* orients in its web and moves toward the source of a vibratory mechanical stimulus when this is of an appropriate rate and amplitude. Thus this method of response to a vibratory stimulus identifies the reaction as a positive taxis. The term tonotaxis would naturally be used in this connection, but since tonotaxis has been used in another way it seems advisable that the terms positive vibrotaxis should be applied if a short descriptive term is desired.

The foregoing may be summarized as follows:

1. *Epeira sclopetaria*, an orb-weaving spider, starting from the center of its web is able to orient, charge and seize flies which strike and are detained in the web. This process is carried out with extreme rapidity.

2. With the aid of a mechanical vibrator it is possible to show that the stimulus is vibratory, the spider orienting to and attacking the vibrator even in the dark.

3. The response can be analyzed into, (*a* the orientation, (*b*) the forward response, and (*c*) the attack on the vibrating object. The response is in essence a positive vibrotaxis.

4. The vibrations are transmitted through the web in all directions from the vibrating point but the intensity (amplitude) decreases toward the center of the web and on either side. The lines of equal intensity of the vibration form roughly a series of circles the centers of which are at the vibrating point.

5. The sense organs used in detecting the stimulus are probably sense hairs on the tarsi.

6. This orb-weaving spider provides itself with a temporary extension of its tactile sense organs which makes its tactile sense in reality a distance receptor, much like an auditory or an olfactory organ.

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EXPLANATION OF PLATE I.

FIG. 1. Showing a female *Epeira sclopetaria* in the normal resting position in the web. The arrow indicates the place where the vibrator straw touches a radial strand of the web.

FIG. 2. The same individual, shown in Fig. 1, orienting to the vibrator which had been in motion for a fraction of a second just before the photograph was taken.

FIG. 1.

FIG. 2.

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EXPLANATION OF PLATE II.

FIG. 3. A spider attacking the vibrator straw while it is in motion.

FIG. 4. A spider in the act of responding to the Y-shaped vibrator. One prong of the vibrator appears in front, the other behind the spider.

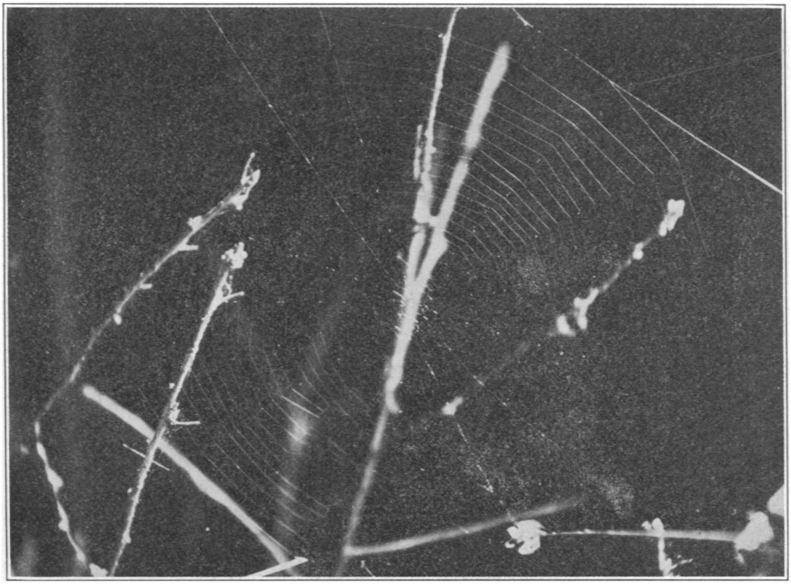

FIG. 3.

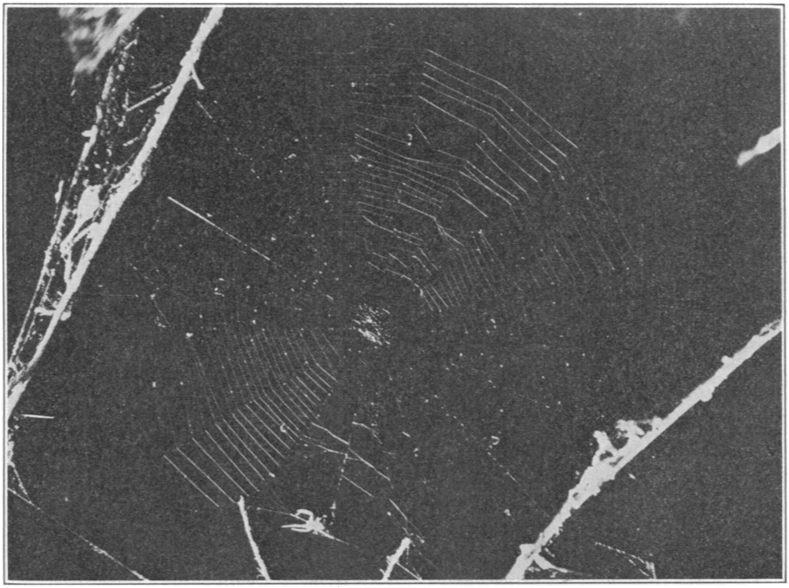

FIG. 4.

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EXPLANATION OF PLATE III.

FIG. 5. A photograph showing the spider in the normal resting position in the web, while the vibrator is in motion. The arrow indicates the place where the vibrator straw touches a radial strand. The doubling or blurring of the lines of the web shows the distribution of the vibrations.

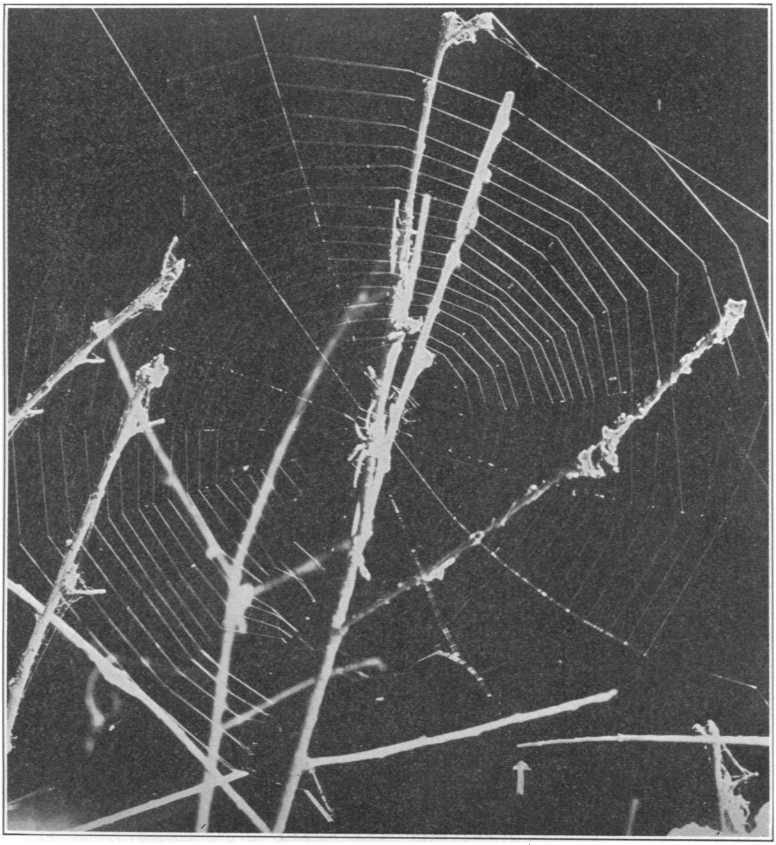

FIG. 5.

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